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Key Points:
- Shallow ponds can be prominent features of salt marsh landscapes but are rarely included in assessments of ecosystem biogeochemistry
- Ponds had similar physical properties but different plant and algal communities, organic matter pools, and oxygen-based metabolism rates
- Ponds may affect marsh carbon dynamics because they have high respiration rates and do not trap or export organic matter on flushing tides

Supporting Information:
- Supporting Information S1

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Shallow ponds are heterogeneous habitats within a temperate salt marsh ecosystem

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Abstract Integrating spatial heterogeneity into assessments of salt marsh biogeochemistry is becoming increasingly important because disturbances that reduce plant productivity and soil drainage may contribute to an expansion of shallow ponds. These permanently inundated and sometimes prominent landscape features can exist for decades, yet little is known about pond biogeochemistry or their role in marsh ecosystem functioning. We characterized three ponds in a temperate salt marsh (MA, USA) over alternating periods of tidal isolation and flushing, during summer and fall, by evaluating the composition of plant communities and organic matter pools and measuring surface water oxygen, temperature, and conductivity. The ponds were located in the high marsh and had similar depths, temperatures, and salinities. Despite this, they had different levels of suspended particulate, dissolved, and sediment organic matter and abundances of phytoplankton, macroalgae, and *Ruppia maritima*. Differences in plant communities were reflected in pond metabolism rates, which ranged from autotrophic to heterotrophic. Integrating ponds into landcover-based estimates of marsh metabolism resulted in slower rates of net production (−8.1 ± 0.3 to −15.7 ± 0.9%) and respiration (−2.9 ± 0.5 to −10.0 ± 0.4%), compared to rates based on emergent grasses alone. Seasonality had a greater effect on pond water chemistry, organic matter pools, and algal abundances than tidal connectivity. Alternating stretches of tidal isolation and flushing did not affect pond salinities or algal communities, suggesting that exchange between ponds and nearby creeks was limited. Overall, we found that ponds are heterogeneous habitats and future expansion could reduce landscape connectivity and the ability of marshes to capture and store carbon.

1. Introduction

Salt marshes support a range of valuable ecosystem services and have some of the highest rates of organic matter (OM) production and storage in coastal environments [*Barbier et al.*, 2010; *McLeod et al.*, 2011]. Refining the role of salt marshes in local and regional carbon budgets requires developing biogeochemical assessments that integrate spatial and temporal heterogeneity [*Hopkinson et al.*, 2012; *McClain et al.*, 2003]. This is becoming increasingly important because natural and man-made disturbances that reduce the productivity of emergent grasses and drainage of marsh soils will likely contribute to an expansion in the number and size of shallow ponds (or pools) that dot the landscape [*Kirwan et al.*, 2008; *Mariotti*, 2016; *Millette et al.*, 2010; *Schepers et al.*, 2017].

Salt marshes include high- and low-elevation areas that are populated by different species of emergent grasses, pockmarked by small ponds, and incised by natural and man-made tidal channels [*Miller and Egler*, 1950]. The ecology and biogeochemistry of emergent grasses, soils, and mudflats have been extensively examined under natural, experimental, and anthropogenically impacted settings for decades, leading to mechanistic descriptions of how marshes function and respond to perturbations. Several factors, including sea level rise and infilling of man-made mosquito ditches, are expected to increase the spatial extent of ponds in the interior of the marsh platform [*Adamowicz and Roman*, 2005; *Kirwan et al.*, 2008; *Wilson et al.*, 2014]. It is unclear how changing habitat composition will affect ecosystem functioning, in part, because key biogeochemical processes that are well characterized in high- and low-marsh habitats are less well understood in ponds.

Permanently inundated ponds are natural features of salt marshes and have been called pools, potholes, and rotten spots in the literature [*Harshberger*, 1909, 1916; *Mariotti*, 2016; *Miller and Egler*, 1950; *Redfield*, 1972].

They can occupy 1–60% of salt marsh platforms [*Adamowicz and Roman*, 2005; *Millette et al.*, 2010; *Schepers et al.*, 2017; *Wilson et al.*, 2014] but are rarely characterized or integrated into whole-ecosystem assessments. These shallow habitats (20–30 cm) range from a few square meters to over several thousand and form through physical (e.g., ice rafting) and biogeochemical processes [*Miller and Egler*, 1950]. Waterlogging of marsh soils, due to increased tidal inundation or reduced drainage efficiency, is a primary catalyst of pond formation because it creates more reducing belowground conditions and initiates dieback of emergent grasses [*Burdick and Mendelssohn*, 1990; *Mendelssohn and McKee*, 1988]. However, other mechanisms, including intense grazing and wrack deposition, can also lead to grass dieback [*Boston*, 1983; *Gedan et al.*, 2009]. Denuded soil patches then deepen and expand through a combination of processes that can include erosion, slumping, compaction, and decomposition of carbon-rich peat [*Ganju et al.*, 2015; *Mariotti and Fagherazzi*, 2013; *van Huissteden and van de Plassche*, 1998]. The relative importance of these different processes in pond development is an open question; decomposition is likely key, but estimates of respiration are scarce [*Johnston et al.*, 2003; *Moseman-Valtierra et al.*, 2016]. Ponds can represent permanent loss of marsh habitat or they can exist for decades before recovering, by draining, being recolonized by emergent grasses, and reaccreting to the initial elevation [*Schepers et al.*, 2017; *Wilson et al.*, 2014]. Consequently, pond formation may reduce OM storage in marsh soils, grass productivity, and OM trapping and likely causes shifts in belowground microbial metabolisms. In combination, these changes have the potential to impact marsh ecosystem functioning and carbon dynamics.

Pond ecology and biogeochemistry are likely influenced by irregular tidal flushing. Ponds are mainly situated in the high marsh and only flushed during spring and storm tides [*Adamowicz and Roman*, 2005; *Millette et al.*, 2010]. In the days-to-weeks between flushing tides, ponds are isolated from new saltwater inputs. During this period, warming and evaporation may concentrate salts and metabolites that, in turn, affect rates of primary production and heterotrophic microbial metabolisms. Tidal flushing may reset the chemistry of surface waters and export algal OM from ponds into tidal creeks and the marsh platform, similar to effect of episodic flood events on floodplain systems [*Ahearn et al.*, 2006; *Tockner et al.*, 1999]. Changes in surface water chemistry caused by irregular tidal flushing likely affect the suitability of ponds as habitat for invertebrates and fish and as foraging grounds for migratory birds [*Heck et al.*, 1995; *Layman et al.*, 2000; *Miller and Egler*, 1950], while export of labile OM may increase connectivity across the marsh landscape by subsidizing nearby food webs.

Characterizing pond biogeochemistry and metabolism is important for improving our current understanding of marsh ecosystem functioning and ability to predict future changes. In this study, we quantified changes in pond ecology and biogeochemistry across tide stages (flushing versus isolation) and seasons (summer versus fall). We tested the hypothesis that tidal isolation would increase surface water salinity and temperature, while flushing would reduce abundances of phytoplankton and macroalgae and concentrations of suspended particulate and dissolved OM. Support for this would suggest that ponds export labile OM and bolster the paradigm that tides increase connectivity across the landscape. We further expected that the likelihood of nighttime hypoxia, or even anoxia, would be greater during tidally isolated periods than when pond surface waters were flushed with new saltwater inputs. Finally, we examined the potential impact of ponding on marsh-ecosystem carbon dynamics by evaluating whether decomposition (i.e., respiration) could be a primary driver of pond expansion and by integrating ponds into estimates of net production and respiration across the marsh platform. We characterized three ponds to determine whether they have similar properties that can be upscaled and extrapolated across the marsh landscape.

2. Methods

We focused on three ponds within the salt marshes of the Plum Island Ecosystems-Long Term Ecological Research (PIE-LTER) site (MA, USA; Figure 1). The marshes experience semidiurnal tides with a mean range of 2.9 m. Emergent vegetation is dominated by *Spartina patens*, short-form *S. alterniflora*, and *Distichlis spicata* in the high marsh (~1.4 m above North American Vertical Datum of 1988 (NAVD88)) and tall-form *S. alterniflora* in the low marsh (~1.0 m above NAVD88) [*Millette et al.*, 2010]. The marsh platform is incised by natural and man-made tidal creeks.

We chose ponds 1, 2, and 3 because they are located at similar elevations in the high marsh (1.44, 1.48, and 1.43 m above NAVD88, respectively), are permanently inundated, have similar depths (0.26–0.30, 0.24–0.29,

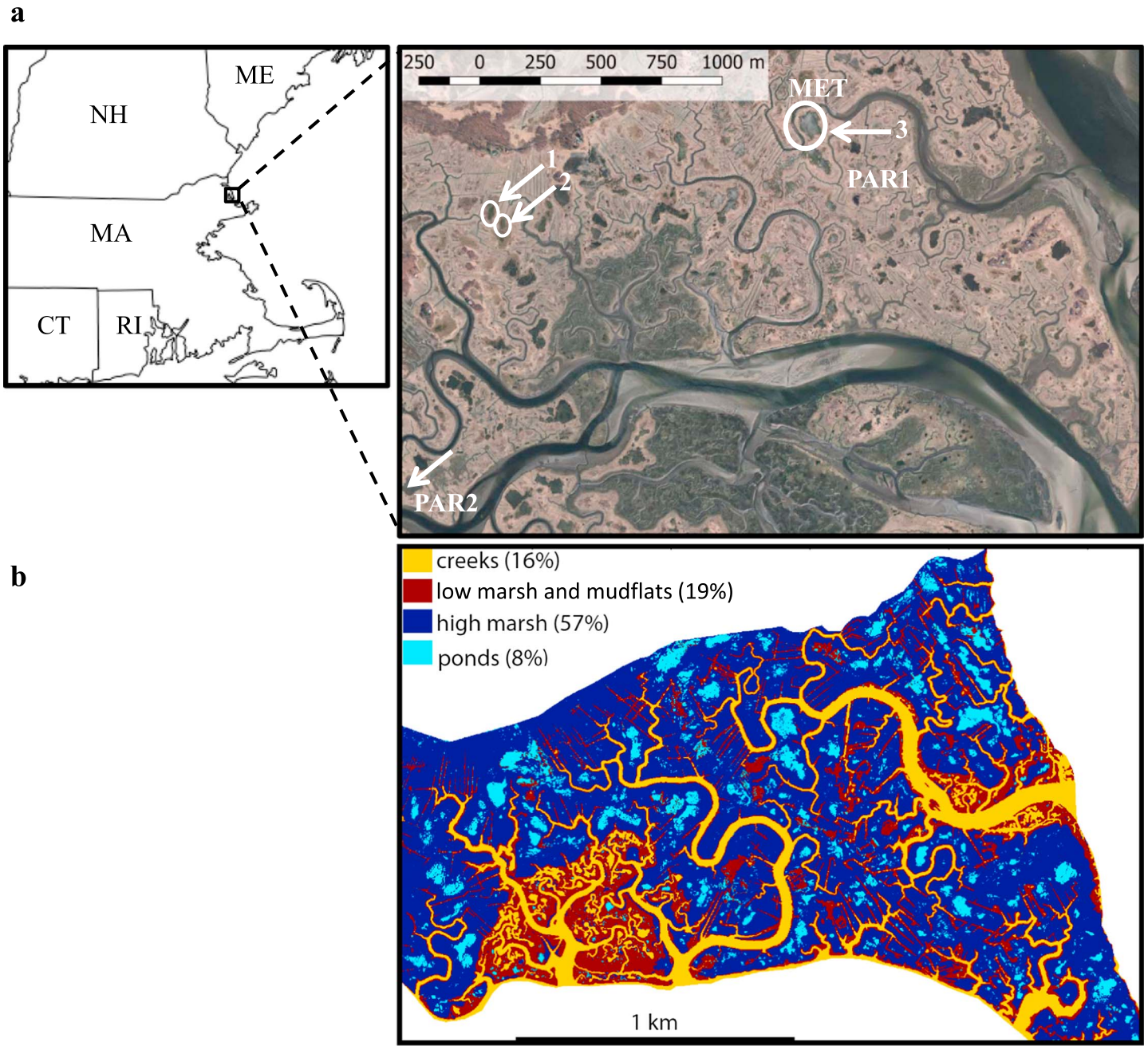

Figure 1. (a) Ponds 1, 2, and 3 are within the high marsh of PIE-LTER, MA, USA. Weather conditions were recorded by a meteorological tower (MET) and photosynthetically active radiation (PAR) was measured at two towers (PAR1 and PAR2). (b) LiDAR was used to calculate the spatial extent of habitat types.

and 0.24–0.29 m, respectively), sediment properties, distinct perimeters (i.e., not connected to other ponds), and are either adjacent to study sites in West Creek (ponds 1 and 2 [*Spivak and Ossolinski*, 2016]) or near a meteorological tower and close to the footprint of an eddy covariance tower (pond 3 [*Forbrich and Giblin*, 2015]). The ponds span a range of surface areas and volumes, which allowed us to determine if properties, like metabolism, scale with dimensions (pond 1: 962 m^2 and 288.6 m^3; pond 2: 643 m^2, 186.5 m^3; 7149 m^2, and 2073.2 m^3). We characterized plant and algal communities, suspended particulate and sediment organic matter (POM and SOM), and surface water chemistry weekly in each pond between 25 June and 13 August and 11–25 November 2014. These 11 sampling events captured alternating periods of tidal flushing and isolation; 3 weeks of flushing were interspersed between 5 weeks of isolation in the summer, while 2 weeks of flushing bookended 1 week of isolation in the fall. Flushing periods were

defined as high tides that overtopped the marsh platform and connected with the ponds, and were based on observations and predicted tide heights. Sensors recording dissolved oxygen (DO), temperature, and conductivity were deployed continuously in each pond from June to November 2014 in order to estimate rates of gross and net ecosystem production (GEP and NEP) and respiration (R). Thus, we captured differences between summer (June–August) versus fall (September–November) and periods of tidal flushing versus isolation.

2.1. Spatial Analyses

High-resolution orthophotos (2014 National Oceanic and Atmospheric Administration, 0.3 m resolution) and LiDAR elevation maps (2014 U.S. Army Corps of Engineers, 0.5 m resolution) were used to classify the marsh study area into four habitats: creeks and ditches, low marsh and mudflats (including drained ponds), permanently inundated ponds, and high marsh. Permanently inundated ponds were identified as locations filled with water during low tide, whereas the other habitats were identified based on their elevation. Single-frame aerial photos (U.S. Geological Survey) indicate that ponds 1 and 2 had started to form by 1978 and pond 3 by 1965. The resolution of earlier photos was too coarse to conclusively identify landscape features (i.e., pond versus mudflat). Later images indicate progressive expansion of all three ponds and suggest that pond development was not abrupt (e.g., ice rafting).

2.2. Pond Plant Communities, Organic Matter Pools, and Surface Water Chemistry

Abundances of macroalgae and the submerged grass *Ruppia maritima* were determined by visually estimating percent cover in six 1 m^2 quadrats placed at three random locations along each of two transects. Sediment cores were collected for chlorophyll (1.5 cm diameter × 1 cm deep) and SOM (5 cm diameter × 2 cm deep) analyses in half of the quadrats. Cores for each analysis were combined in precombusted (450°C) glass vials to form composite samples. Surface water was collected in 1 L precombusted glass bottles and filtered through either precombusted and preweighed glass fiber filters (chlorophyll and POM), or Rhizon samplers (Rhizosphere products; dissolved organic carbon (DOC), nitrate, and ammonium). Rhizons were used for dissolved analytes in order to compare the composition of surface and pore waters.

Sediment and surface water chlorophyll were analyzed according to *Neubauer et al.* [2000]. POM filters were dried to constant mass (60°C), weighed for total particulates, and prepared for elemental analyses (total organic carbon (TOC) and nitrogen) by fuming with hydrochloric acid (HCl) to remove carbonates. SOM samples were dried to a constant mass, homogenized with a Retsch Mixer Mill 200, and fumed with HCl. The TOC and nitrogen content of POM filters and sediments were measured by the Stable Isotope Laboratory at the Marine Biological Laboratory. POM was calculated by normalizing TOC to the volume of water filtered. Surface water DOC was determined by high-temperature combustion [*Lalonde et al.*, 2014]. Surface water nitrate ranged from $<$0.1 to 2.1 μM, but levels were often below detection and are not reported.

2.3. Environmental Conditions in the Ponds and Salt Marsh

Sensors deployed in the ponds recorded DO (% saturation), temperature (°C), and conductivity (mS cm^{-1}) in 15 min intervals. A YSI 6-series or EXO2 was deployed in pond 3 from 8 May to 25 November (0–50 ± 0.1 mg DO L^{-1}, −5–50°C, 0–200 ± 1% mS cm^{-1}). The EXO2 conductivity sensor failed on 13 November and measurements after 12 November were discarded. A combination of YSI 6-series, EXO2, and HOBO DO (U26-001, 0–30 ± 0.5 mg DO L^{-1}), conductivity (U24-002-C, 0.1–55 ± 0.05 mS cm^{-1}), and temperature (UA-002-64, −20–70°C) loggers were deployed from 19 June to 7 July in ponds 1 and 2. From then until 25 November, only HOBO sensors were deployed in ponds 1 and 2. Different deployments reflect sensor availability. Sensors were situated at middepth above patches of bare sediment and regularly inspected, cleaned, and calibrated according to manufacturer specifications. When possible, we deployed a freshly calibrated sensor before collecting an older one in order to cross calibrate. Salinity (practical salinity unit (psu)) was calculated from conductivity and temperature using manufacturer software. DO (mg L^{-1}) was calculated from % saturation, barometric pressure, salinity, and temperature [*Garcia and Gordon*, 1992].

Atmospheric conditions were recorded by three meteorological towers (Figure 1). Wind speed (m s^{-1}), temperature (°C), relative humidity (%), and barometric pressure (mbar) were measured 14 m above the marsh (42.742° N, 70.830° W). Photosynthetically active radiation (PAR; μmol m^{-2} s^{-1}) was recorded by

Table 1. Pond Temperatures and Salinities Across Seasons and Tide Stages[a]

a.

		Temperature (°C)				Salinity (psu)			
		Summer		Fall		Summer		Fall	
Tide Stage	Pond	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Flushing	1	24.56	0.33	13.60	0.97	24.02	0.27	29.71	0.54
	2	23.61	0.38	13.57	0.92	27.18	0.64	26.61	0.32
	3	20.87	0.41	15.47	1.09	27.69	0.23	28.61	0.67
Isolated	1	26.32	0.28	13.87	1.02	26.03	0.63	30.75	0.53
	2	26.07	0.30	14.03	1.00	28.55	0.54	27.54	0.39
	3	22.99	0.41	18.24	0.78	28.35	0.33	31.14	0.49

b.

	Pond		Season		Tide		Pond × Season		Pond × Tide		Season × Tide		P × S × T		r^2	
Response	F	p	F	p	F	p	F	p	F	p	F	p	F	p	Cond.	Mar.
$\log_{10}$ Temperature (°C)	1.21	0.300	185.20	<**0.001**	6.30	**0.012**	12.73	<**0.001**	0.89	0.410	21.45	<**0.001**	1.89	0.151	0.34	0.33
$\log_{10}$ Salinity (psu)	0.97	0.380	56.27	<**0.001**	0.54	0.463	28.42	<**0.001**	0.04	0.963	0.03	0.867	0.18	0.832	0.95	0.19

[a]Average daily temperatures and salinities in ponds 1, 2, and 3 (a). Differences in water temperatures and salinities across seasons (summer versus fall), tide stages (flushing versus isolated), and ponds were detected using linear mixed effect models (b). The marginal (mar) and conditional (cond) r^2 reflect the variance explained by fixed effects alone or by fixed and random effects combined, respectively. Data were transformed as indicated. Significant results ($p < 0.05$) are in bold. SE = standard error.

two towers that were deployed at different times between May and November (42.724°N, 70.856°W and 42.739°N, 70.827°W).

2.4. Data Analyses

To detect changes in pond plant communities and OM pools between tide stages (flushing versus isolated) and seasons (summer versus fall) we constructed linear mixed effect models using the nlme package for the software R [*Pinheiro et al.*, 2016]. The mixed models evaluated the fixed effects of pond, tide stage, and season. To account for differences in sensors measuring pond temperature and conductivity, we included sensor identity as a nested random effect within sampling time point. We further specified a first-order autoregressive correlation structure with the same random structure to account for our repeated measures sampling design. By modeling covariances among data points sampled within ponds, a mixed model approach allows us to meet the assumption of independence of errors. For each model, we calculated the marginal (variance of fixed effects only) and conditional (variance of both fixed and random effects) r^2 (in the sense of *Nakagawa and Schielzeth* [2013]), using the piecewiseSEM package in R [*Lefcheck*, 2016].We used a "free-water" diel oxygen approach to estimate GEP, NEP, and R in the ponds [*Staehr et al.*, 2010]. Oxygen saturation was calculated using volumetric solubility constants and corrected for salinity, temperature, and barometric pressure [*Garcia and Gordon*, 1992]. Wind speeds measured at 14 m were scaled to 10 m height [*Smith*, 1985]. Gas transfer velocities (k, m d^{-1}) were calculated according to *Cole and Caraco* [1998] and adjusted using a Schmidt number for oxygen in salt water [*Wanninkhof*, 2014]. GEP, NEP, and R were estimated from measurements of PAR, water temperature, and DO using an ordinary least squares approach with the LakeMetabolizer package in R [*Winslow et al.*, 2016]. Rates were not estimated for days with missing data (e.g., maintenance). Differences in metabolic rates across ponds, tide stages, and seasons were detected using linear mixed models with a specific autocorrelation structure, as described above.

To evaluate the sources of surface water DOC and the factors influencing GEP, NEP, and R, we constructed linear mixed models as described above, but with potential drivers as fixed effects and pond identity as a random effect. The potential sources of DOC included sediment chlorophyll, macroalgae, *R. maritima*, SOM, and POM. The potential drivers of metabolic rates included water temperature and salinity, PAR, sediment chlorophyll, macroalgae, *R. maritima*, SOM, and POM. We did not include surface water chlorophyll in either model because concentrations were correlated to suspended POM. DOC was excluded from the metabolism models because concentrations were positively correlated to macroalgae. Both models include SOM and sediment chlorophyll because these variables were not correlated to one another. A separate model was conducted evaluating the relationship between pond R and surface water DOC. For each model, we calculated the marginal and conditional r^2 (as detailed above).

Table 2. Statistical Results for Pond Organic Matter Pools and Plant Community Properties[a]

	Pond		Season		Tide		Pond × Season		Pond × Tide		Season × Tide		P × S × T		r^2	
Response	F	p	F	p	F	p	F	p	F	p	F	p	F	p	Cond.	Marg.
Surface Water Organic Matter																
log_{10} DOC (μmol L^{-1})	33.12	**<0.001**	22.73	**0.003**	7.82	**0.031**	38.16	**<0.001**	14.47	**0.001**	3.18	0.125	1.92	0.197	0.96	0.78
log_{10} POM (μmol C L^{-1})	21.73	**<0.001**	11.70	**0.011**	0.00	0.984	3.80	**0.048**	0.34	0.720	0.02	0.886	1.13	0.352	0.85	0.59
log_{10} POM (molar C:N)	21.98	**<0.001**	0.28	0.611	0.70	0.432	2.08	0.162	1.35	0.292	0.02	0.900	0.78	0.476	0.72	0.50
Sediment Organic Matter																
TOC (μmol mg dry sed^{-1})	39.25	**<0.001**	0.73	0.422	1.08	0.333	0.47	0.634	0.85	0.448	0.38	0.555	0.78	0.476	0.75	0.68
C:N (molar)	5.17	**0.021**	3.47	0.105	0.68	0.438	0.63	0.549	0.04	0.961	0.04	0.854	0.23	0.800	0.45	0.37
Primary Producers																
log_{10} Surface water chlorophyll (μg L^{-1})	10.41	**0.002**	14.86	**0.004**	1.15	0.311	2.58	0.117	0.74	0.497	0.03	0.866	1.48	0.267	0.84	0.56
log_{10} Sediment chlorophyll (μg cm^{-2})	2.01	0.176	0.00	0.979	0.76	0.405	1.07	0.372	0.13	0.877	2.12	0.179	0.49	0.623	0.24	0.24
log_{10} *R. maritima* (% cover)	103.04	**<0.001**	5.12	0.058	0.39	0.551	0.53	0.588	1.02	0.363	0.05	0.834	0.73	0.482	0.63	0.61
log_{10} Macroalgae (% cover)	8.32	**<0.001**	32.78	**<0.001**	2.06	0.195	1.13	0.326	0.23	0.792	0.34	0.578	0.63	0.535	0.39	0.36

[a]Differences in pond organic matter (OM) pools and plant community properties, across seasons and tide stages, were detected using linear mixed effect models. The marginal (mar) and conditional (cond) r^2 reflect the variance explained by fixed effects alone or by fixed and random effects combined, respectively. Data were transformed as indicated. Significant P values (<0.05) are in bold.

Data were log_{10}-transformed as necessary to maintain homogeneity of variance. Values are presented as means ± standard error (SE). Statistical analyses were performed using R open-source software [*R Development Core Team*, 2016].

3. Results

3.1. Environmental Conditions

The study area encompassed 305.8 ha, of which 57% was high marsh; 19% was low marsh, mudflats, and drained ponds; 16% was tidal creeks and ditches; and 8% was permanently inundated ponds (Figure 1b).

Weather conditions in 2014 were comparable to 2013 and 2015. During the study months (June–November), precipitation in 2014 (53 cm) was higher than in 2013 (41 cm) but comparable to 2015 (50 cm), while average air temperatures were comparable across 2013–2015 [*Giblin and Garritt*, 2013, 2014, 2015].

Water temperatures were similar across ponds but were warmer in the summer and during isolated tidal periods (Table 1 and Figures S1a–S1d in the supporting information). Temperature differences between tide stages were stronger in the summer, and the seasonal temperature transition was greater for ponds 1 and 2 than for pond 3. Salinity was similar across ponds and tide stages but differed between seasons; salinity increased from summer to fall in ponds 1 and 3, but decreased in pond 2 (Table 1 and Figures S1e–S1h). Overall, the ponds had similar water temperatures and salinities and only temperature was affected by alternating periods of tidal flushing and isolation.

3.2. Organic Matter (OM) Pools

Surface water and sediment OM pools showed different trends across ponds, tide stages, and seasons (Table 2 and Figure 2). In the summer, surface water DOC (μmol L^{-1}) was highest in ponds 1 and 2 and during periods of tidal isolation (Table 2 and Figure 2a). In the fall, however, DOC levels were lower and similar across ponds and tide stages. Suspended POM (μmol C L^{-1}) changed seasonally, being highest in ponds 1 and 2 in the summer and lower and similar across all ponds in fall but did not vary with tidal stage (Figure 2b). The carbon:nitrogen ratio (C:N, molar) of POM was consistently higher in ponds 1 and 2, compared to pond 3, and did not vary with season or tide stage (Figure 2c). Sediment TOC (μmol C mg dry $sed.^{-1}$) was lowest, while C:N ratios were highest in pond

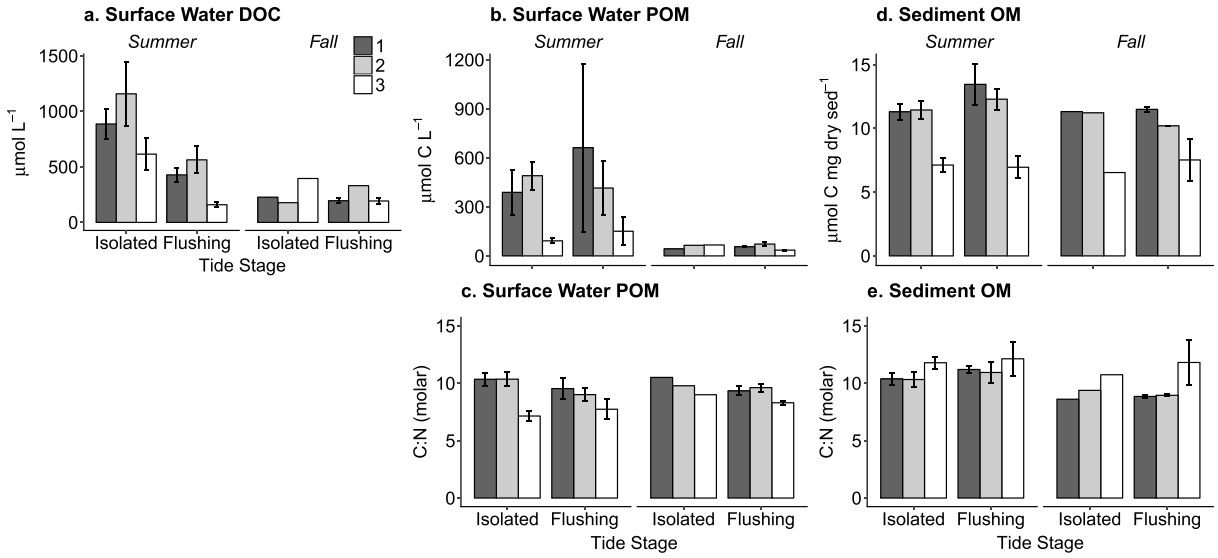

Figure 2. (a) Surface water DOC concentrations as well as the carbon content and C:N ratio of suspended (b and c) particulate organic matter (POM) and (d and e) sediment OM (SOM) were measured in ponds 1, 2, and 3 (black, grey, and white bars, respectively) during periods of tidal isolation and flushing in summer and fall. Data were collected weekly between 25 June and 13 August and 11–25 November 2014. In the summer this included 3 weeks of tidal flushing interspersed between 5 weeks of tidal isolation. In the fall, 2 weeks of flushing bookended 1 week of isolation. The error bars are SE of the mean. See Table 2 for statistical results.

3 (Figures 2d and 2e). Overall, ponds 1 and 2 had higher OM concentrations (summer only for DOC and POM) and higher-quality SOM (lower C:N), but lower quality suspended POM (higher C:N), than pond 3.

3.3. Primary Producer Communities

The main primary producers were surface water and sediment microalgae, the submerged grass *R. maritima*, and the macroalgae *Ulva* (Table 2 and Figure 3). Surface water chlorophyll (µg L^{-1}) was highest in ponds 1 and 2 in the summer (Figure 3a), while sediment chlorophyll (µg cm^{-2}) was similar across ponds and seasons (Figure 3b). The % cover of *R. maritima* was highest in pond 1 and lowest in pond 3, while macroalgal

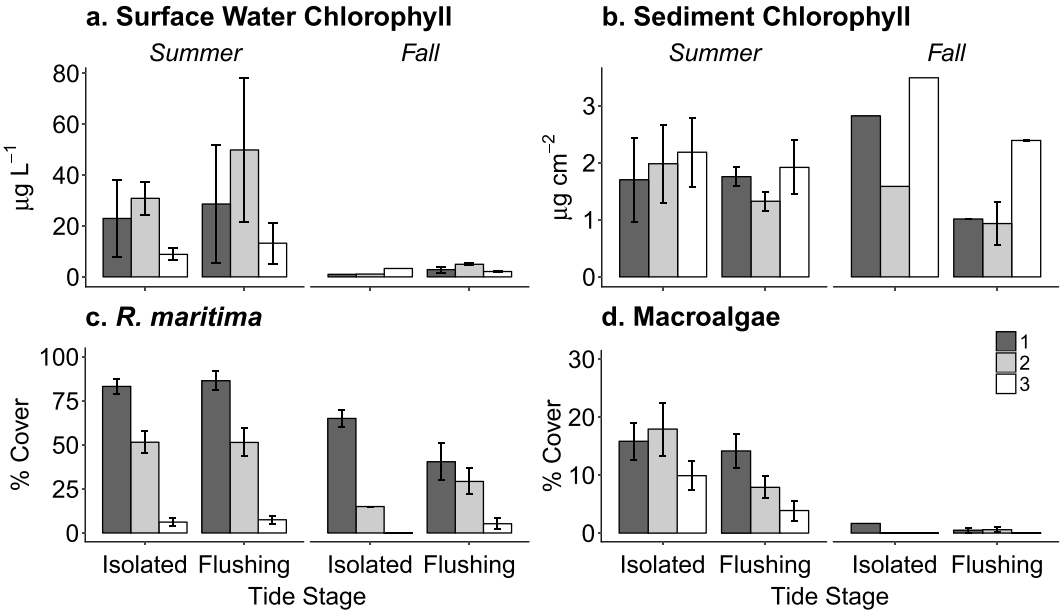

Figure 3. Chlorophyll in (a) surface waters and (b) sediments and macrophyte percent cover (c and d, note differences in the % cover scales) were measured in ponds 1, 2, and 3 (black, grey, and white bars, respectively) during periods of tidal isolation and flushing in summer and fall. Data were collected weekly, as described in Figure 2. The error bars are SE of the mean. See Table 2 for statistical results.

Table 3. Statistical Results for Pond Metabolic Rates Across Seasons and Tides[a]

Response ($mg\ O_2\ L^{-1}\ d^{-1}$)	Pond		Season		Tide		Pond × Season		Pond × Tide		Season × Tide		P × S × T		r^2	
	F	p	F	p	F	p	F	p	F	p	F	p	F	p	Cond.	Mar.
log_{10} GEP	79.20	<**0.001**	56.90	<**0.001**	8.39	**0.004**	5.45	**0.005**	2.16	0.119	0.06	0.802	2.68	0.119	0.73	0.33
log_{10} NEP	71.99	<**0.001**	7.99	**0.005**	0.53	0.467	20.85	<**0.001**	3.94	**0.021**	0.46	0.500	0.28	0.757	0.61	0.24
log_{10} R	0.52	0.596	38.59	<**0.001**	10.23	**0.002**	5.20	**0.006**	1.92	0.149	0.49	0.487	2.14	0.121	0.54	0.19
log_{10} GEP: R	75.74	<**0.001**	5.91	**0.030**	0.09	0.767	7.22	**0.001**	4.08	**0.019**	0.09	0.764	0.75	0.472	0.62	0.23

[a]Differences in gross ecosystem production (GEP), net ecosystem production (NEP), respiration (R), and the ratio of GEP:R across ponds, seasons, and tide stages were detected using linear mixed effect models. The marginal (mar) and conditional (cond) r^2 reflect the variance explained by fixed effects alone or by fixed and random effects combined, respectively. Data were transformed as indicated. Significant results ($p < 0.05$) are in bold.

abundances were similar in ponds 1 and 2 and lower in pond 3 (Figures 3c and 3d). Macroalgal cover decreased sharply from summer to fall while seasonal changes in *R. maritima* were less pronounced ($p = 0.058$). Overall, there were clear differences in plant communities between ponds and seasons, but abundances did not change with tide stage.

3.4. Whole-Pond Metabolism Rates

Oxygen-based rates of metabolism were calculated for 158 days in pond 1, 150 days in pond 2, and 187 days in pond 3. The number of observations per pond varied because of differences in deployment dates, and we omitted days with incomplete records of temperature, salinity, or oxygen (e.g., sensor maintenance). DO ($mg\ L^{-1}$) ranged from near zero to supersaturated in summer (range 0–24.9 in pond 1, 0–22.5 in pond 2, and 0.5–12.2 in pond 3) and fall (range 0–20.6 in pond 1, 0–18.0 in pond 2, and 0.6–11.8 in pond 3; Figures S1i–S1l). Over the entire study, hypoxic conditions (DO $< 2\ mg\ L^{-1}$) occurred on 94 (59%) nights in pond 1, 89 (59%) nights in pond 2, and 54 (29%) nights in pond 3. There was a higher incidence of hypoxia in summer (pond 1: 90% of nights, pond 2: 89%, and pond 3: 39%) than in fall (pond 1: 39%, pond 2: 42%, and pond 3: 10%). Hypoxic conditions also varied with tide stage. The frequency of hypoxia was 1.5 (pond 1) to 3.1 (pond 3) times greater in the summer and 2.3 (pond 2) to 100 times (pond 3) greater in the fall, during periods of tidal isolation than flushing.

Whole-pond metabolism rates ($mg\ O_2\ L^{-1}\ d^{-1}$) varied across ponds, tide stages, and seasons (Table 3 and Figures 4 and S2). GEP was highest in the summer in ponds 1 and 2, and rates were slower in the fall, particularly in pond 2 which had the strongest seasonal change (Figure 4a). NEP was positive in pond 1, negative in pond 3, and switched from autotrophy to heterotrophy between summer and fall in pond 2 (Figure 4b). R was similar across ponds, and rates were faster in the summer than fall. Tidal isolation led to higher rates of R (ponds 1 and 3) and GEP (pond 3) in the summer. The ratio of GEP:R, an index of autotrophy:heterotrophy, was consistently highest in pond 1 and lowest in pond 3; the ratio decreased from summer to fall in ponds 1 and 2 only (Figure 4d).

4. Discussion

Despite similarities in environmental setting (i.e., high marsh and atmospheric conditions) and physical properties (i.e., water depth, salinity, and temperature), there was considerable heterogeneity in OM pools, plant communities, and metabolism rates across ponds (Tables 1–3 and Figures 2–4). Greater similarities between ponds 1 and 2 than pond 3 suggest that spatial factors (e.g., seed dispersal distance and creek identity) may be important determinants of pond ecology and biogeochemistry. Differences in pond plant communities, that may have arisen from spatial factors, likely affected the balance between net autotrophy and heterotrophy as well as the frequency of hypoxia. Alternating periods of tidal isolation and flushing did not affect pond salinities or OM pools (except DOC; Tables 1 and 2 and Figures 2 and 3), suggesting that there was limited exchange between ponds and tidal creeks. However, warmer temperatures (Table 1), greater incidence of hypoxia, and faster R rates (ponds 1 and 3; Figure 4c) indicate that pond conditions changed during tidal isolation and affected metabolic fluxes. The effects of tide stages were clearer in summer than fall but, in general, were much weaker than changes in season. Overall, we found that ponds are heterogeneous and semiisolated habitats that neither import or export OM and have limited connectivity with the landscape. Consequently, predicting the current and future effects of ponds on marsh ecosystem functioning will

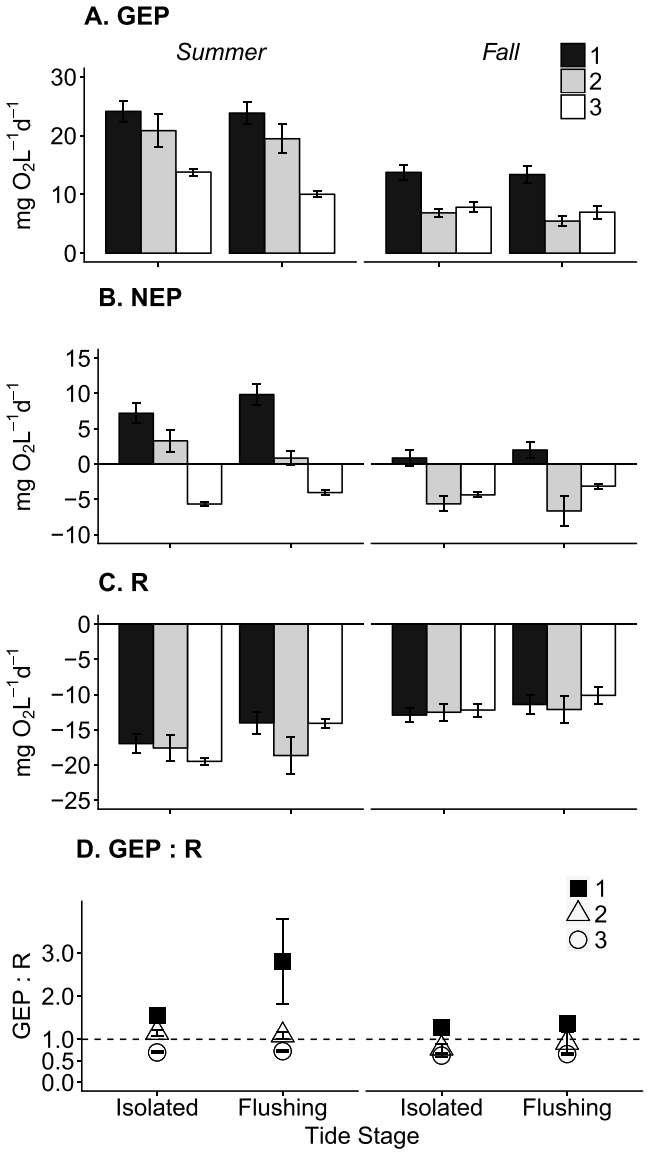

Figure 4. Rates of (a) gross ecosystem production (GEP), (b) net ecosystem production (NEP), and (c) respiration (R), and the (d) ratio of GEP:R were measured in three high-marsh ponds during periods of tidal isolation and flushing, in summer and fall. Data for ponds 1, 2, and 3 are represented by black, grey, and white shading (Figures 4a–4c) and squares, triangles, and circles (Figure 4d), respectively. Metabolic rates were calculated from sensor data of DO, temperature, and conductivity recorded in 15 min intervals between June and November 2014. The error bars are SE of the mean. See Table 3 for statistical results.

require a more developed understanding of how ponds are both affected by landscape heterogeneity (e.g., tidal creek identity) and drivers of it.

4.1. Tidal Exchange and Pond Biogeochemistry

Tides play an important role in shaping the ecology, geomorphology, and biogeochemistry of salt marshes but had somewhat limited effects on pond properties and processes. Differences arising from tide stages were only evident in the summer when periods of tidal isolation created conditions (e.g., warmer temperatures and more DOC; Tables 1 and 2 and Figure 2a) that stimulated respiration (Table 3 and Figure 4c). Faster respiration rates likely contributed to the greater frequency of nighttime hypoxia during isolated tides because rapid depletion of surface water oxygen was not offset by inputs of creek water. The effects of tide stages on pond temperatures and salinities were small in comparison to seasonality and the influence of storm events, like 1.78 cm of rainfall on 16 October 2014 (salinity only; Figure S1h and Table 1). The limited effects of alternating tide stages on surface water salinity may reflect incomplete exchange, similarities between ponds, tidal creeks [20–27 psu; *Deegan et al.*, 2007], and Rowley River [19–32 psu; *Hopkinson et al.*, 1999], or subsurface inputs. The latter seems unlikely, however, since pore water percolation is low in high-marsh habitats and only affects surface soils at high tide [*Gardner and Gaines*, 2008; *Howarth and Giblin*, 1983; *Howes and Goehringer*, 1994]. This is the first study to characterize continuous changes in pond temperatures and salinities across tide stages and seasons. Water temperatures averaged across tide stages in the PIE-LTER ponds (Table 1) were similar to summertime values in New Jersey marsh ponds [*Hunter et al.*, 2009] but slightly cooler than in Virginia ponds during summer and fall [*Layman et al.*, 2000]. Salinities were similar across tide stages in the PIE-LTER ponds (Table 1) but increased during tidally isolated periods in several Texas marsh ponds [*Miller et al.*, 2009]. These comparisons suggest that the effects of seasonality and tidal exchange on pond salinity and temperature are likely stronger in wetlands at lower latitudes, where irradiance and evaporation are more intense.

The absence of tide effects on levels of suspended POM, surface water chlorophyll, and macroalgae indicates that ponds have a limited role in lateral OM exchange (Figures 2b and 3a and 3d and Table 2). Higher levels of

POM and algae during flushing periods would have suggested both resuspension of pond sediments and trapping of OM delivered from tidal creeks and the marsh platform. Alternatively, higher levels of POM and algae during isolated periods might have indicated that accumulated carbon was exported on flushing tides. Our results contrast with other episodically flooded ecosystems, such as floodplains, where algal biomass accumulates during periods hydrologic isolation and is subsequently exported downstream where it contributes to carbon budgets and supports microbial and animal food webs [*Ahearn et al.*, 2006; *Schemel et al.*, 2004].

Ponds were likely a small source of DOC to the landscape in the summer, as concentrations were higher during isolated tide stages than when the ponds were flushed (Figure 2a and Table 2). Macroalgal abundances were positively correlated to DOC concentrations, suggesting that this algal community was an important source of dissolved OM to pond surface waters ($p < 0.001$; Table S1 in the supporting information). Positive correlations between DOC concentrations and R ($p = 0.007$, marginal $r^2 = 0.62$, conditional $r^2 = 0.96$) suggest that greater OM availability stimulated R. This effect was clearest during tidally isolated periods in summer in ponds 1 and 3 (Figures 2a and 4c). The phenomenon of DOC accumulating during hydrologic isolation also occurs in floodplain lakes [*Tockner et al.*, 1999; *Valett et al.*, 2005] while the stimulatory effect of DOC on R has been observed in lakes [*Hanson et al.*, 2003]. Although ponds exported DOC, similar levels of surface water POM and algae between tide stages suggest that ponds are not important integrators of OM washed from the landscape or sources of carbon to adjacent marsh and tidal creek habitats.

4.2. Controls on Primary Producer Communities

The abundances and distribution of plants and algae across the three ponds likely reflect a combination of abiotic factors, including nutrient recycling and seed dispersal, rather than top-down control by herbivores. The inorganic nitrogen requirements and uptake rates of *R. martima* and *Ulva* are much higher [*Pedersen and Borum*, 1997; *Thursby*, 1984a, 1984b; *Thursby and Harlin*, 1984] than concentrations of nitrate and ammonium in pond surface waters (<0.1–2.1 μmol NO_3^{-1} L^{-1} and 0.5–7.5 μmol NH_4^{+} L^{-1}) and tidal creeks (1.9–4.8 μmol NO_3^{-1} L^{-1} and 8.6–18.1 μmol NH_4^{+} L^{-1} [*Spivak and Ossolinski*, 2016]). This suggests that abundant plant and algal communities were likely supported by internal nitrogen stores [*Pedersen and Borum*, 1996] and tight recycling between autotrophic and heterotrophic communities. This latter mechanism is consistent with GEP:R of ~1, particularly in pond 2 (Figure 4d).

The striking variation in *R. maritima* and macroalgal coverage across ponds cannot be ascribed to differences in depths, salinities, temperatures, or physical sediment properties (e.g., bulk density; Table 1). It is unlikely that water clarity was important, since *R. maritima*, which cannot grow under low light conditions [*Orth and Moore*, 1988], was more abundant in ponds 1 and 2 where POM and surface water chlorophyll levels were highest (Figures 2b and 3a and 3c). Instead, differences in pond plant communities may reflect limited dispersal of seeds and propagules due to incomplete tidal exchange and slow water velocities. Seeds from submerged grasses and macroalgal spores rapidly settle out of surface waters and dispersal distances depend on current velocities and animal vectors [*Charalambidou et al.*, 2003; *Gaylord et al.*, 2002; *Orth et al.*, 1994]. In the marsh platform, dispersal of emergent grass seeds can be highly localized and patterns of seed density and adult plants are tightly coupled [*Rand*, 2000]. The close proximity of ponds 1 and 2 likely facilitated exchange of grass seeds and algal propagules (Table 2 and Figures 1a and 3a, 3c, and 3d), but flushing tides may not effectively transport reproductive tissues to ponds across the landscape.

Frequent periods of hypoxia (Figures S1i–S1l) are consistent with low dissolved oxygen concentrations measured over several nights in other PIE-LTER marsh ponds [*Johnston et al.*, 2003] and in Virginia Coastal Reserve-LTER marsh ponds [*Layman et al.*, 2000]. Recurring hypoxia likely made the ponds toxic to many animals and reduced grazing pressure on plants. Grazing effects would have been clearest during periods of tidal isolation when other food resources were not available, as has been seen in floodplain lakes [*Keckeis et al.*, 2003]. However, submerged grass and algal abundances were similar between flushing and isolated periods (Table 2 and Figure 3). Many herbivorous invertebrates and omnivorous fishes that inhabit marsh ponds are sensitive to oxygen availability and recurring hypoxia likely limited their activities and survivorship [*Heck et al.*, 1995; *Layman et al.*, 2000]. Overall, our data hint at a series of complex processes underlying patterns of primary producer abundance. Identifying specific mechanisms controlling plant and algal communities will be key for integrating ponds more fully into assessments of marsh ecosystem ecology and biogeochemistry.

4.3. Drivers of Pond Metabolism

Oxygen-based rates of pond metabolism were largely driven by abiotic factors (temperature, PAR, and salinity) and macrophyte abundances (macroalgae, *R. maritima*), but were not sensitive to levels of suspended POM, SOM, or sediment algae (Table S2). Patterns of NEP, GEP, and GEP:R across the ponds mirrored differences in macroalgal and *R. maritima* coverage (Figures 3c and 3d and 4a, 4b, and 4d). Pond 1 had the highest plant coverage and was net autotrophic, while pond 3 had lower abundances of macroalgae and *R. maritima* and was heterotrophic (Figures 3c and 3d and 4b and 4d). Pond 2 had intermediate *R. maritima* coverage and switched from autotrophy to heterotrophy between summer and fall. The different patterns of NEP and GEP across ponds, but similar R rates, suggest that the balance between autotrophy and heterotrophy was driven by plant communities rather than decomposition. This is consistent with positive relationships between rates of production and macroalgal (NEP $p = 0.006$ and GEP $p = 0.055$) and *R. maritima* (NEP $p = 0.005$ and GEP $p = 0.055$) coverage, but a lack of correlation between plant abundances and R (Table S2). Instead, R increased with water temperatures ($p < 0.001$) and salinities ($p = 0.014$), which were similar across ponds (Table 1). Interestingly, R was not correlated with sediment TOC ($p = 0.814$; Table S2), which has been used in first-order rate models to predict decomposition and pond deepening [*van Huissteden and van de Plassche*, 1998]. Although our data only reflect dynamics in three ponds, they suggest that metabolic rates may vary in a predictable way with abiotic conditions (temperature, PAR, and salinity) and plant abundances, but not with pond dimensions (i.e., depth, surface area, and volume). Consequently, understanding controls on plant distributions may be key for extrapolating metabolic rates across ponds and the landscape. Further, positive correlations between metabolic rates and temperature (GEP $p < 0.001$, R $p < 0.001$) and PAR (NEP $p = 0.050$) suggest that production and R may vary across latitudinal gradients and that rates may increase in the future as the climate warms.

Our estimates of pond metabolism were comparable to short-term measurements from other PIE-LTER marsh ponds [*Johnston et al.*, 2003] as well as to rates in Plum Island Sound [*Vallino et al.*, 2005], estuaries [*Caffrey et al.*, 2014], and coastal sediments [*Tucker et al.*, 2014] but much higher than many lakes [*Hanson et al.*, 2003] floodplain systems [*Gallardo et al.*, 2012], and coastal lagoons [*Ávila-López et al.*, 2017]. A caveat is that our metabolism estimates only reflect processes that consume and produce oxygen and miss some anaerobic (e.g., sulfate reduction) and physical processes (e.g., ebullition). Consequently, oxygen-based R rates are likely underestimates since oxygen concentrations regularly fell to hypoxic levels. Sensor error may have also affected our results since the wide swings in DO saturation tested the bounds of sensor accuracy. Further, gas exchange parameterizations are a main source of uncertainty in gas-based metabolism estimates and the model we used was developed for lake systems.

4.4. Ponds in a Marsh-Ecosystem Context

The contribution of ponds to the metabolism of salt marsh ecosystems remains a key unknown. Often metabolism rates reported for marshes only reflect emergent grasses and soils. To evaluate how accounting for ponds could affect estimates of marsh metabolism, we calculated rates of NEP and R that combined measurements from the ponds (Figures 4b and 4c) with published rates for the PIE-LTER marshes [*Forbrich and Giblin*, 2015]. In the marsh, rates of daytime NEP (summer -339 ± 11.5; fall -123 ± 12 mmol CO_2 m^{-2} d^{-1}) and nighttime R (summer 325 ± 8.8; fall 173 ± 11 mmol CO_2 m^{-2} d^{-1}) were measured using eddy covariance from May to October 2014 (PAR1 tower in Figure 1a). We made the simplifying assumption that rates of marsh NEP and R represent emergent grasses and soils only. We then combined marsh and pond rates, based on the % land cover of each in Figure 1b. The calculated rates of combined pond-marsh NEP and R were lower than rates based on vegetation alone (NEP % difference: summer -8.1 ± 0.32 to -11.9 ± 0.07, fall -9.4 ± 0.74 to -15.7 ± 0.87; R % difference: summer -5.1 ± 0.44 to -5.9 ± 0.31; fall: -2.9 ± 0.50 to -10.0 ± 0.41). This suggests that estimates of whole-ecosystem metabolism, that are extrapolated from rates that only reflect emergent grasses and soils, likely overestimate both NEP and R. Further refinement of the role of shallow ponds in whole ecosystem metabolism requires longer-term measurements of NEP and R in more ponds, evaluating whether pond-air gas exchange varies with plant community composition and pond water chemistry (e.g., DOC), as well as estimates of anaerobic metabolisms and dissolved gas export from ponds by tides.

A crucial question related to pond formation and expansion is the importance of organic matter decomposition. Pond depths reflect a combination of processes, including peat decomposition and accretion of the

surrounding marsh platform. The marsh platform in this system accretes at a rate of rate of 2.5 mm yr^{-1} and gained 9–12 cm of elevation, since the ponds began to form in 1978 (ponds 1 and 2) and 1965 (pond 3) [*Wilson et al.*, 2014]. This elevation gain accounts for 30–42% of the depth in ponds 1 and 2 and pond 3, respectively. In order for the ponds to reach their current dimensions, decomposition of the underlying peat would need to occur at average rates of 43–73 g C m^{-2} yr^{-1} (assuming soil bulk density and carbon content are 0.18 g cm^{-3} and 7%, respectively) [*Deegan et al.*, 2012]. These decomposition rates agree well with NEP measured in ponds 2 and 3, extrapolated over an entire year. This suggests that the combined effects of vertical accretion and peat decomposition are a plausible mechanism for pond formation and expansion, and is consistent with an earlier study [*Johnston et al.*, 2003]. Net autotrophy in pond 1 does not support this conclusion and underscores the caveat that metabolism rates likely change over time and vary with plant abundances and community composition. Further, it is likely that sulfate reduction, an anaerobic metabolism not reflected by DO fluxes, is a key driver of peat decomposition and pond morphology [*van Huissteden and van de Plassche*, 1998]. Despite these caveats, our data indicate that high rates of R in ponds may have a greater impact on long-term carbon storage in marshes than on annual rates of ecosystem metabolism. In the future, combining estimates of aerobic and anaerobic metabolisms, accretion rates, and SOM composition may be useful in refining the role of decomposition in pond development and marsh carbon budgets.

5. Conclusions

Overall, ponds are biogeochemcially heterogeneous systems that are minimally influenced by tides. Despite similar physical characteristics (i.e., elevation, water depth, salinity, and temperature; Table 1) ponds differed in OM pools (surface water and sediment), plant and algal abundances, and oxygen-based rates of metabolism (Tables 2 and 3 and Figures 2–4). The limited effects of alternating periods of tidal isolation and flushing suggest that ponds at temperate latitudes have predictable salinity regimes and neither integrate OM washed from the landscape nor export carbon to nearby habitats. Our data further suggest that plant and algal abundances are controlled by a combination of abiotic factors. However, a greater understanding of pond nutrient dynamics and plant dispersal mechanisms will be key for predicting distributions of primary producers in ponds across the landscape and important for further refining the role of ponds in marsh metabolism. High pond R rates likely affect both marsh geomorphology, by contributing to pond expansion, and ecology, by creating hypoxic conditions and limiting habitat for aquatic animals (Figures S1i–S1l) [*Bolduc and Afton*, 2004; *Layman et al.*, 2000]. Future expansion of pond spatial extent, in response to sea level rise and land management practices, may therefore reduce the ability of marshes to capture and store carbon. Draining ponds by connecting them to tidal channels or ditch networks may offset these negative effects by promoting recolonization by emergent grasses and rapid soil accretion [*Wilson et al.*, 2014]. However, increasing the drainage efficiency of the marsh platform may promote soil aeration, decomposition, and subsidence [*Portnoy and Giblin*, 1997], which, in turn, may make marshes more susceptible to storms and rising seas. In the future, careful management of ponds may be opportunities to maximize valuable ecosystem services.

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